



Restoration of broadleaved forest vegetation – early plant colonization in plantations on former fields



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CONTENTS

ABSTRACT	4
INTRODUCTION	5
METHODS	6
<i>STUDY AREA</i>	<i>6</i>
<i>COLLECTING DATA</i>	<i>7</i>
<i>MANAGEMENT OF THE STANDS</i>	<i>8</i>
<i>DATA ANALYSES</i>	<i>8</i>
RESULTS	10
<i>SPECIES DENSITY</i>	<i>10</i>
<i>ISOLATION</i>	<i>12</i>
<i>TREE SPECIES</i>	<i>12</i>
<i>STAND-WISE APPROACH</i>	<i>12</i>
<i>Oak stand 41b</i>	<i>13</i>
<i>Oak stand 16n</i>	<i>14</i>
<i>Oak stand 49a</i>	<i>15</i>
<i>Oak stand 2e</i>	<i>17</i>
<i>Beech stand 45d</i>	<i>17</i>
<i>Beech stand at Torup</i>	<i>18</i>
<i>SPECIES-WISE APPROACH</i>	<i>18</i>
<i>DISPERSAL MODE</i>	<i>20</i>
DISCUSSION	22
<i>MIGRATION RATES</i>	<i>22</i>
<i>MAXIMUM COVER AND FREQUENCY</i>	<i>24</i>
<i>SPECIES RICHNESS AND STAND AGE</i>	<i>25</i>
<i>DISTURBANCE AND LIGHT CONDITIONS</i>	<i>25</i>
<i>BORDER BETWEEN PLANTATIONS AND OLD FOREST AND EFFECTS OF FRAGMENTATION</i>	<i>26</i>
<i>SOIL CONDITIONS AND SEED BANK</i>	<i>27</i>
CONCLUSION	28
IMPLICATIONS	28
REFERENCES	29
APPENDIX 1	31
APPENDIX 2	32
APPENDIX 3	33
APPENDIX 4	34
APPENDIX 5	35
APPENDIX 6	36
APPENDIX 7	37

Abstract

The purpose of this study was to evaluate the colonization patterns of forest herb layer species in newly established plantations on former arable fields. Among six stands surveyed the following hypotheses were tested:

1. Species richness is higher in new stands adjacent to older forest than in isolated ones
2. Oak stands provide better conditions for colonization than beech stands due to more suitable light conditions
3. Differences in migration rates are related to the diaspore dispersal mode of the plant species

The maximum possible migration rates for the stands measured varied between 4.7 m year⁻¹ and 69.9 m year⁻¹. The maximum realized migration rates ranged from 0.37 to 66.0 m year⁻¹ and the mean migration rates varied from 0.37 to 8.2 m year⁻¹. These migration rates are consistently higher than the results presented in previous similar studies. The species richness was higher in adjacent stands compared to isolated stands and new oak stands contained more species than beech stands where only a few of the fast colonizers were found. The results showed that the migration of different forest herb layer species is influenced by the diaspore dispersal mode, special border characteristics between older forest and young plantations and the light conditions depending on the tree species planted. The fringe between the older stand and the new plantation should be long and without roads and open vegetation in order to enhance successful forest plant colonization. Concerning the ability of plants to colonize new stands soon after canopy closure, conditions are generally more favorable in oak stands than in beech stands, probably mainly due to differences in light availability.

Key words: beech, dispersal mode, forest herbs, isolation, migration rate, oak

Introduction

Before the human settlement started to influence the appearance of ancient forest, fragmentation in the natural landscape was mainly caused by water, mountains, forest fires or other natural landscape forms or disturbances, rather than by fields, roads and urbanized areas. The former kind of fragmentation made the vegetation more diverse in a natural way and there was always a connection between vast woodland areas where plant and animal species could migrate. With the industrial revolution and the increase in human populations more and more agricultural land was needed to support the development. Therefore woodland areas were turned into agricultural land and fragmentation increased with decreasing forest cover. In parts of southern Sweden, many woodlands are today separated by vast areas of fields and human settlements. This kind of fragmentation is not sustainable due to the small scale of the remaining forest patches and their isolation which may create insuperable colonization conditions for most of the forest herb species.

However, more and more agricultural land is afforested in Sweden nowadays. In the southern part the climate (oceanic) and a large human population (high need for recreation) favors the establishment of deciduous forests. Both, former agricultural land and forest land is often planted with broadleaved trees. For amenity and biodiversity it is important to achieve a species rich understorey in new plantations. When discussing successful restoration of broadleaved stands the question arises if the plants are able to colonize new stands. And if they do, how long time does it take, what factors influence the colonization and is the species pool influenced by the former land use (Honnay et al 2002a)?

In older, more natural forests (often called ancient forest) shrubs, herbs and trees are found which in new plantations are often absent. Several studies have shown the lack of diversity in the flora of isolated stands compared to those adjacent to older woodland (e.g. Brunet 2004; Bossuyt et al 1999; Brunet & von Oheimb 1998a, Flinn & Vellend 2005). Therefore, in order to establish plantations as similar as possible to natural forest, it is essential to avoid fragmentation of forest areas and encourage the establishment of forest herb layer species.

Much work has been done previously in studying the migration of woodland herbaceous plants as well in the United States of America, for instance by Matlack G. R., and in Europe by e.g. Brunet J., Bossuyt B., Hermy M., Dzwonko Z., von Oheimb G. and Honnay O. In order to enhance broadleaved forest restoration, more studies will be needed, especially considering the herb layer and the colonization abilities of different species. Previous studies have probably underestimated the migration abilities of forest herb layer species due to limitations concerning high stand age and small stand size.

The current study provides new data about forest herb colonization by analyzing four pedunculate oak *Quercus robur* and two European beech *Fagus sylvatica* stands (described in the first section in the Methods part). A combination of relatively large stand size and young stand age provided the opportunity to reveal

higher realized migration rates than in previous studies. More exact data about the migration speed of different forest herb species could be calculated by a full-scale survey of each stand (see Data Collection in Methods part). The Results part gives an overview about the most important outcome of the collected data. In the Discussion part the relevant topics concerning colonization speed, dispersal mode, species richness and different factors influencing migration of herbal species are discussed. A comparison of the results from this study with previous work is presented at the end of the discussion part. Appendices include a picture of each stand and a map of the surveyed area.

The goal of this thesis was to study the colonization potential of herbaceous forest plants in young oak and beech plantations on arable land.

The following hypotheses were tested:

1. Species richness is higher in new stands adjacent to older forest than in isolated ones
2. Oak stands provide better conditions for colonization than beech stands due to more suitable light conditions
3. Differences in migration rates are related to the diaspore dispersal mode of the plant species

Methods

Study area

The study sites are located in southernmost Sweden (55°32'N, 13°11'E) at the Skabersjö and Torup estates, Skåne County. The mean annual temperature in the area is about 7.5°C and the annual rainfall is approximately 650 mm. The altitude of the sites varies from 25 m to 75 m a.s.l. Most of the old woodlands in the area are dominated by European beech *Fagus sylvatica* and to a lesser extent by pedunculate oak *Quercus robur*. A unique set of forest stands regarding the number, size and distance from colonization sources were established on arable land between 1990 and 1995. These woods can be regarded as a large “field experiment” which allows to analyze colonization processes under comparatively uniform conditions regarding climate and soil (Brunet 2004).

The study sites were selected based on their low age, relatively large size and a varying location considering the contiguity of older forest stands with source populations (see appendices 1-7). Two isolated oak stands, one slightly and one strongly isolated (distance to nearest old woodland 900m) and two oak stands contiguous with older forest were chosen. To compare effects of the tree species planted, two contiguous beech stands were also selected. All sites have been established on former arable land. Almost no hedges or open ditches exist in the study area, therefore almost all source populations for colonizing forest plants are found in older forests. Arable land usually does not contain forest plants in

the soil seed bank (Brunet & von Oheimb 1998a). The size of the stands varied from 2.8 ha to 3.7 ha, except for the beech stand at Torup, which had a size of 10.4 ha. The age of the stands, calculated from the year of tree planting, varied from 15 to 18 years (Table 1).

Collecting data

Transects along the planting rows were set throughout the plantations. The distance between each row was usually about one meter. By walking in the middle (Fig. 1), three rows were inspected and the size (in m²) of the patch of the selected shade tolerant herbaceous plant species and its center GPS-coordinates were recorded. In case of larger individuals (e.g. *Dryopteris* ssp., *Athyrium filix-femina* etc.), the number of plants was recorded. The species list from which, in case of presence, the species were recorded is shown in Table 2. The list includes typical forest herbaceous plants, mainly according to Schmidt et al. (2003, group 1.1).

The GPS device used was a GARMIN eTrex Vista HCx. The RT90 (Swedish National Grid 1990) was used with the accuracy of the GPS-receiver stated +/- 3m at the site. The data were collected during May and June 2008 when both spring- and summer species were present.

Table 1. An overview of the stands studied. Stand origin: P, planted; S, sown; PCT, pre-commercial thinning.

Number of the site	Establishment, year	Size (ha)	Distance to older forest (m)	Fringe to older forest	Management	Stand origin
41 b oak	1990	3.46	0	Yes	PCT 2008	P
16 n oak	1992	2.93	0	Yes	PCT 2008	S
49 ab oak	1991	3.53	0	No	PCT 2008	S
2e oak	1992	3.72	900	No	PCT 2007	S
45d beech	1991	2.82	0	Yes	80% removal of larch recently	P
Torup beech	1993	10.40	0	Yes	Removal of birch recently	P

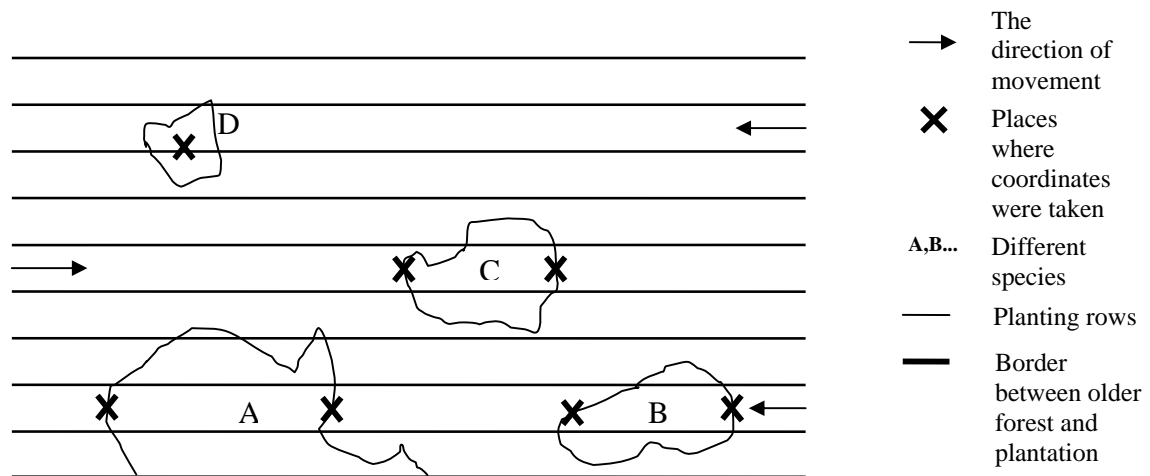


Fig. 1. A schematic overview of the field data collection.

Management of the stands

All oak stands were thinned recently (spring of 2007 or 2008). In the beech stand 45d most of the larch as a shelter tree was cut not more than 3 years before this survey was conducted. In the Torup beech stand, birch as the shelter tree was cut entirely a few years ago. As oak stands were thinned manually, no significant harm was done to the understorey flora. Marks of cutting activities in beech stands were evident, whereas vegetation had recovered.

Data analyses

The number of shade tolerant herbaceous forest species present in the recent woods was compared with the species present in the adjacent older forest stands. Species diversity was also compared between oak and beech stands, and between contiguous and isolated stands, respectively.

By using GIS tools, the distance from the nearest older woodland border to each colonizing patch was measured. For those of the herbaceous plants studied that had not spread until the far edge of the stand, the farthest patch was determined and measured. Yearly migration rates were calculated by dividing the distances by the age of the stand for all species with four or more occurrences in a stand. As the age of the stand is calculated from the planting time of the trees, the colonization rates are possibly underestimates because many plant species may start to establish just after the canopy closure which in the present study happened just a few years ago (Matlack 1994).

Table 2. Shade-tolerant herbaceous forest species (mainly according to Schmidt et al 2003) which are known from the study area (Brunet 2007) and which in case of presence were recorded in the stands surveyed. Species marked with (*) were not recorded during the survey.

Species	Species
<i>Actaea spicata</i> *	<i>Gymnocarpium dryopteris</i> *
<i>Adoxa moschatellina</i>	<i>Hepatica nobilis</i> *
<i>Allium ursinum</i>	<i>Lamiastrum galeobdolon</i>
<i>Anemone nemorosa</i>	<i>Luzula pilosa</i>
<i>Anemone ranunculoides</i> *	<i>Maianthemum bifolium</i>
<i>Athyrium filix-femina</i>	<i>Melica uniflora</i>
<i>Brachypodium sylvaticum</i> *	<i>Mercurialis perennis</i>
<i>Bromus benekenii</i> *	<i>Milium effusum</i>
<i>Campanula trachelium</i> *	<i>Oxalis acetosella</i>
<i>Carex sylvatica</i>	<i>Paris quadrifolia</i> *
<i>Circaea lutetiana</i>	<i>Poa nemoralis</i>
<i>Convallaria majalis</i>	<i>Polygonatum multiflorum</i>
<i>Corydalis intermedia</i>	<i>Pulmonaria obscura</i>
<i>Dryopteris carthusiana</i>	<i>Pyrola minor</i>
<i>Dryopteris filix-mas</i>	<i>Ranunculus ficaria</i>
<i>Elymus caninus</i>	<i>Sanicula europaea</i> *
<i>Epipactis helleborine</i>	<i>Scrophularia nodosa</i>
<i>Festuca gigantea</i>	<i>Stachys sylvatica</i>
<i>Gagea lutea</i>	<i>Stellaria nemorum</i>
<i>Gagea spathacea</i> *	<i>Stellaria holostea</i>
<i>Galium odoratum</i>	<i>Viola reichenbachiana</i>

Migration rates were calculated in three ways. 1) Maximum migration rates are calculated by dividing the distance between the farthest individual from the closest edge of the probable source population and the age of the stand (Matlack 1994). 2) The maximum frequency rates (in m year^{-1}) show the migration rates at those distances from the older forest where a species attained maximum frequency (no. occurrences in distance classes). 3) Maximum cover rates were calculated for the distance from the older forest border to the distance class with the highest cover (Matlack 1994, in m^2 for small plants and in number of plants for ferns and *Epipactis helleborine*).

The relation between migration rates of species analysed in both Brunet & von Oheimb (1998a) and in this study were studied with Pearson correlation analysis (Minitab 15 statistical package).

Some of the species are difficult to classify into dispersal modes. In this work, various authors were compared to classify species (e.g. Brunet 2007, Brunet & von Oheimb 1998, Brunet 2004 and Hermy et al 1999). The opinions of different authors matched in general. *Poa nemoralis* and *Milium effusum* were ambiguous though. Brunet & von Oheimb (1998a) stated for *Milium effusum* not to have a certain dispersal agent; but Brunet (2007) stated it to be adhesive. Hermy et al (1999) stated that *Poa nemoralis* is wind dispersed, Brunet (2007) considered it

to be adhesive to animal fur. It seems that seeds of *M. effusum* and *P. nemoralis* can be dispersed together with their flowers which easily attach to fur or feathers (pers. comment Jörg Brunet). The distribution of species within dispersal modes in plantations and older adjacent forest was compared with the chi-square test (Minitab 15 statistical package).

Results

Species density

The species density of forest plants varied considerably between the stands (Table 3). The most species rich stand was the contiguous 41b oak plantation with 20 shade tolerant species (63% of the total species pool of all surveyed stands). However, the second contiguous oak stand, 16n, only contained 11 (34%) species. The slightly isolated oak stand 49ab had eight (25%) species. The most isolated oak stand, 2e, had the lowest number of species of interest, two species which corresponds to only 6% out of the total number of species in the surveyed stands. In the two beech stands (45d and Torup) the colonization success was fairly low compared to the oak stands. Eight (25%) species out of 32 were recorded in 45d and six (19%) species were found in Torup.

Six species of the older adjacent forest stands (19%) did not colonize the newly established plantations (Table 3). These species represent the dispersal modes ingested seeds (*Convallaria majalis*, *Maianthemum bifolium*), adhesive seeds (*Elymus caninus*, *Stachys sylvatica*) or ant-dispersed seeds (*Melica uniflora*, *Pulmonaria obscura*). However, three forest species were present only in plantations but were absent in the adjacent older forests surveyed (*Carex sylvatica*, *Luzula pilosa* and *Pyrola minor*).

The most successful colonizers, both in space and time, were the ferns. All three species recorded (*Athyrium filix-femina*, *Dryopteris filix-mas* and *Dryopteris carthusiana*) were present in most of the stands and in large populations throughout the area. However, in the isolated oak stand 2e all these three species were absent in spite of their fast colonization abilities. The orchid *Epipactis helleborine* showed a good capability in colonizing new stands as well. Although the general number of plants that were recorded was low, the migration rate was very high.

Table 3. Species present in the surveyed stands (first column, in bold) and in the closest adjacent older forest stands (2nd column, Brunet, unpublished data) at the Skabersjö and Torup estates, southern Sweden. The diaspore dispersal type is also given.

Species	41b oak		16n oak		49ab oak		2e oak		45d beech		Torup beech		Dispersal type
<i>Adoxa moschatellina</i>	x	x				x		x	x	x			Ingested
<i>Allium ursinum</i>		x	x	x				x					Ants
<i>Anemone nemorosa</i>		x	x	x		x		x	x	x		x	Ants
<i>Athyrium filix-femina</i>	x	x		x	x	x			x	x	x	x	Wind
<i>Carex sylvatica</i>	x												Ants
<i>Circaea lutetiana</i>	x	x			x	x		x		x		x	Adhesive
<i>Convallaria majalis</i>		x		x				x		x		x	Ingested
<i>Corydalis intermedia</i>	x	x							x				Ants
<i>Dryopteris carthusiana</i>	x	x	x	x	x	x		x	x	x	x	x	Wind
<i>Dryopteris filix mas</i>	x	x	x	x	x	x		x	x	x	x	x	Wind
<i>Elymus caninus</i>				x		x				x		x	Adhesive
<i>Epipactis helleborine</i>	x	x			x				x	x	x		Wind
<i>Festuca gigantea</i>	x	x	x	x		x	x	x		x		x	Adhesive
<i>Gagea lutea</i>		x	x	x						x		x	Ants
<i>Galium odoratum</i>	x	x				x		x		x		x	Adhesive
<i>Lamium strumarium</i>	x	x						x		x		x	Ants
<i>Luzula pilosa</i>	x												Ants
<i>Maianthemum bifolium</i>		x				x				x		x	Ingested
<i>Melica uniflora</i>		x				x				x		x	Ants
<i>Mercurialis perennis</i>		x	x	x								x	Ants
<i>Milium effusum</i>	x	x	x	x	x	x		x		x		x	Adhesive
<i>Oxalis acetosella</i>	x	x		x		x		x		x		x	Auto
<i>Poa nemoralis</i>		x	x	x	x	x	x	x		x	x	x	Adhesive
<i>Polygonatum multiflorum</i>	x	x		x						x		x	Ingested
<i>Pulmonaria obscura</i>				x						x			Ants
<i>Pyrola minor</i>	x												None
<i>Ranunculus ficaria</i>		x	x	x		x		x	x	x		x	Ants
<i>Scrophularia nodosa</i>	x	x		x	x	x				x		x	None
<i>Stachys sylvatica</i>				x						x		x	Adhesive
<i>Stellaria holostea</i>	x	x	x	x		x		x		x	x	x	None
<i>Stellaria nemorum</i>	x	x		x		x		x		x		x	Ingested
<i>Viola reichenbachiana / riviniana</i>	x	x		x		x		x		x		x	Ants/none
Total no. of species 32	20	26	11	21	8	19	2	17	8	26	6	24	
% of colonization from total species pool	63	81	34	66	25	59	6	53	25	81	19	75	

Isolation

Forest species density decreased with increasing isolation from the older forest. As can be seen in Fig. 2, the oak stands have a decreasing species number with increasing isolation. In the beech stands the same pattern can be noticed although in very small scale. They both are adjacent to older forest stands, yet the border characteristics might have some influence. In stand 45d the border between the older stand and the plantation was a small forest road, whereas in Torup the border was a rather wide grassland.

Tree species

The adjacent beech stands tended to have less forest species than the adjacent oak stands (Fig. 2). Out of the 45 species x site combinations in the four adjacent stands, only 31% of the combinations were found in the two beech stands.

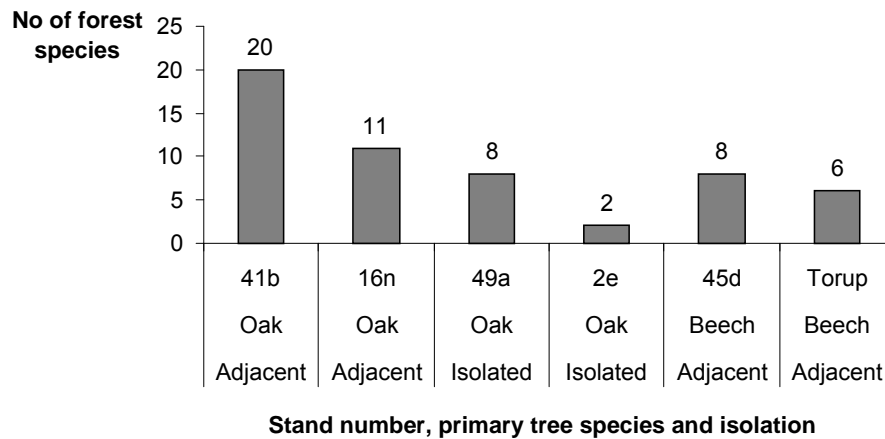


Fig. 2. The species density of forest plants in recent oak and beech plantations at the Torup and Skabersjö estates, southern Sweden.

Stand-wise approach

As all of the surveyed stands differ in size and habitat characteristics, the colonization rates should be considered stand wise. The maximum possible migration rates for the stands varied between 4.7 m year⁻¹ in 41b and 69.9 m year⁻¹ in the strongly isolated 2e, 9.8 m year⁻¹ could be calculated for 45d, 11.7 m year⁻¹ for 16n, 22.9 m year⁻¹ for Torup and 18.8 m year⁻¹ for 49a. The maximum realized migration rates ranged from 0.37 to 66.0 m year⁻¹ and the mean colonization rates varied from 0.37 to 8.2 m year⁻¹.

Oak stand 41b

The number of forest species was highest in this stand and many species attained high frequencies; therefore a large number of colonization rates could be calculated.

The maximum realized migration rates in 41b ranged from 0.37 to 4.69 m year⁻¹ (Table 4). The most successful species are *Dryopteris filix-mas* and *Milium effusum*. *Poa nemoralis* (4.64 m year⁻¹), *Stellaria holostea* (4.54 m year⁻¹) and *S. nemorum* (4.44 m year⁻¹) showed a remarkable migration ability as well. Most of the fast colonizers (e.g. ferns, *Circaea lutetiana*) have reached the far end of the stand although in some cases the border between the plantation and the older forest has not been actively colonized (Fig. 3). *Corydalis intermedia* and *Oxalis acetosella* have low migration rates (0.37 and 0.61 m year⁻¹ respectively). The migration rates at maximum frequency and maximum cover vary from 0.29 to 4.41 meters year⁻¹.

Table 4. Annual migration rates based on the farthest individual, the maximum frequency and the maximum cover in the oak stand 41b.

Species	Max. migration rate (m/y)	Migration rate at max. frequency (m/y)	Migration rate at max. cover (m/y)	Dispersal mode
<i>Dryopteris filix-mas</i>	4.44	2.65	0.29	Wind
<i>Milium effusum</i>	4.43	4.41	4.41	Adhesive
<i>Poa nemoralis</i>	4.38	2.65	4.41	Adhesive
<i>Stellaria holostea</i>	4.28	0.88	0.29	None
<i>Stellaria nemorum</i>	4.19	0.29	0.29	Ingested
<i>Circaea lutetiana</i>	3.76	2.65	3.82	Adhesive
<i>Athyrium filix-femina</i>	3.76	0.88	0.88	Wind
<i>Dryopteris carthusiana</i>	3.57	2.65	2.65	Wind
<i>Epipactis helleborine</i>	3.26	0.88	0.88	Wind
<i>Lamium galeobdolon</i>	2.29	0.88	0.88	Ants
<i>Polygonatum multiflorum</i>	1.96	2.06	2.06	Ingested
<i>Adoxa moschatellina</i>	1.47	0.88	1.47	Ingested
<i>Oxalis acetosella</i>	0.58	0.29	0.29	Auto
<i>Corydalis intermedia</i>	0.35	0.29	0.29	Ants

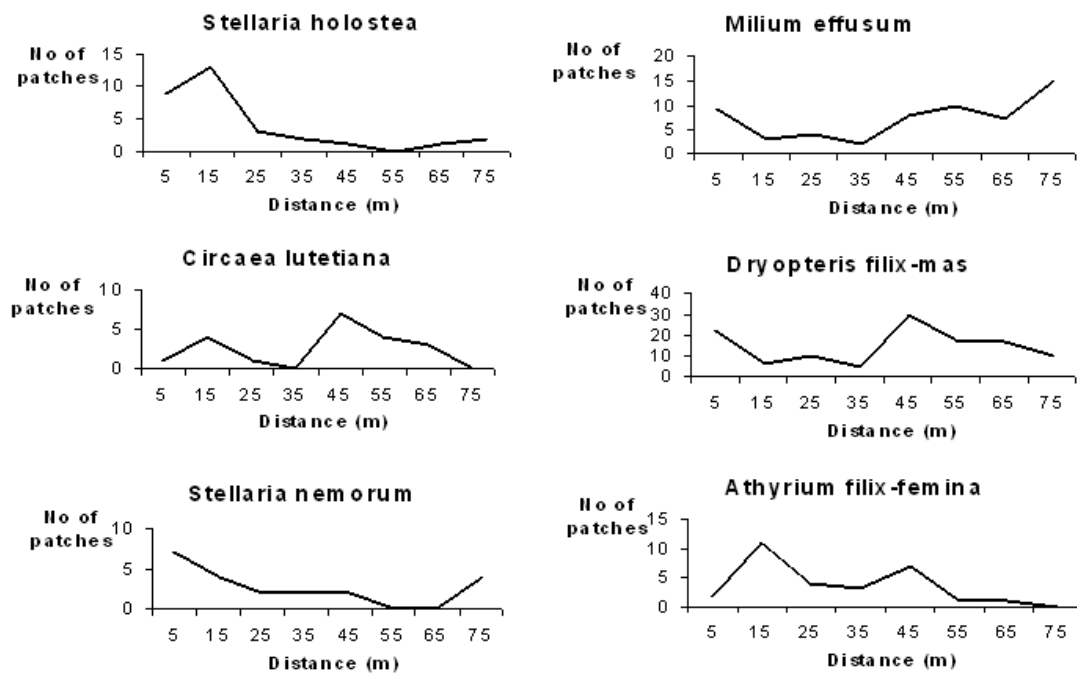


Fig. 3. Colonization patterns of *Stellaria holostea*, *Milium effusum*, *Circaea lutetiana*, *Dryopteris filix-mas*, *Stellaria nemorum* and *Athyrium filix-femina* in the oak stand 41b.

Oak stand 16n

In oak stand 16n the distances for the colonization rates for the farthest individual, maximum cover and maximum frequency were calculated i) from a small corner in the northern part, ii) two sides at the North-East direction and iii) from the edge between them (direction South-East) where the potential colonization populations were located (Appendix 2).

Migration rates could be calculated for seven species (Table 5). *Mercurialis perennis* and *Ranunculus ficaria* had a maximum dispersal speed of only 1.25 and 1.32 m year⁻¹, respectively. The other species showed much higher speed: *Poa nemoralis*, *Milium effusum* and *Dryopteris filix-mas* all had migrated more than seven m year⁻¹ (7.51, 7.24 and 7.00 m year⁻¹, respectively). *Festuca gigantea* showed rates of 5.25 m year⁻¹ and *Stellaria holostea* 2.91 m year⁻¹. In stand 16n the highest frequency of *Poa nemoralis* is found near the border and the frequency is decreasing with increasing distance (Fig. 4).

Table 5. Annual migration rates based on the farthest individual, the maximum frequency and the maximum cover in the oak stand 16n.

Species	Max. migration rates (m/y)	Migration rate at max frequency (m/y)	Migration rate at max cover (m/y)	Dispersal mode
<i>Poa nemoralis</i>	7.51	0.31	0.94	Adhesive
<i>Milium effusum</i>	7.24	0.31	0.31	Adhesive
<i>Dryopteris filix-mas</i>	7.00	2.19	2.19	Wind
<i>Festuca gigantea</i>	5.25	4.69	4.69	Adhesive
<i>Stellaria holostea</i>	2.91	0.31	2.81	None
<i>Ranunculus ficaria</i>	1.32	0.31	0.31	Ants
<i>Mercurialis perennis</i>	1.25	0.31	0.31	Ants

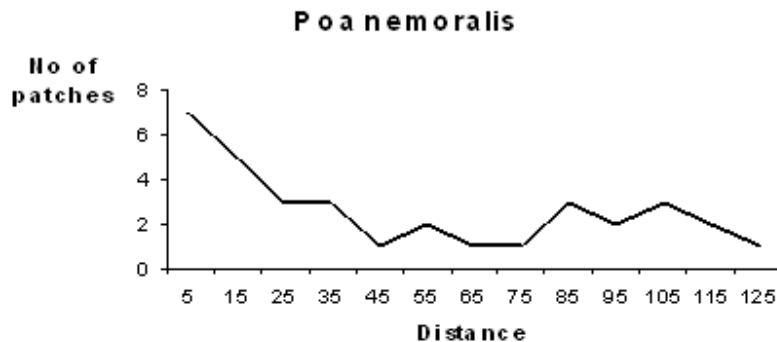


Fig. 4. The colonization pattern of *Poa nemoralis* in the oak stand 16n.

Oak stand 49a

The migration rates were calculated excluding the northeastern strip of the stand, as this part was situated behind an *Abies nobilis* plantation, which resulted in a higher degree of isolation than for the main part of the stand.

The stand 49a is connected with an older oak forest only with a common edge in the south east (Appendix 3). Therefore one might presume that the number of plants present is rather low. Four species out of the 19 forest species found in the older adjacent stand were recorded in four or more patches (Table 6). The total number of the species that colonized the stand was eight. Due to a low frequency the migration rates of *Dryopteris carthusiana*, *Epipactis helleborine*, *Milium effusum* and *Scrophularia nodosa* were not calculated. The other four species *Athyrium filix-femina*, *Circaea lutetiana*, *Dryopteris filix-mas* and *Poa nemoralis* showed very high colonization ability (16.6, 15.9, 15.9 and 13.6 m year⁻¹ respectively). *Circaea lutetiana* showed a pattern which is common to the fast colonizers (Fig. 5). This species was absent from the closest distances from the border but present in the farthest points from the probable colonization source. The rest of the species had an unchanged or decreasing frequency with

an increasing distance from the border of the older forest. The colonization patterns of *Poa nemoralis*, *Circaea lutetiana* and *Dryopteris filix-mas* are presented in Fig. 5.

Table 6. Annual migration rates based on the farthest individual, the maximum frequency and the maximum cover in the oak stand 49a.

Species	Max. migration rate (m/y)	Migration rate at max. frequency (m/y)	Migration rate at max. cover (m/y)	Dispersal mode
<i>Circaea lutetiana</i>	16.56	12.06	12.06	Adhesive
<i>Poa nemoralis</i>	15.91	8.53	5.59	Adhesive
<i>Dryopteris filix-mas</i>	15.91	5.00	5.00	Wind
<i>Athyrium filix-femina</i>	13.59	13.82	12.65	Wind

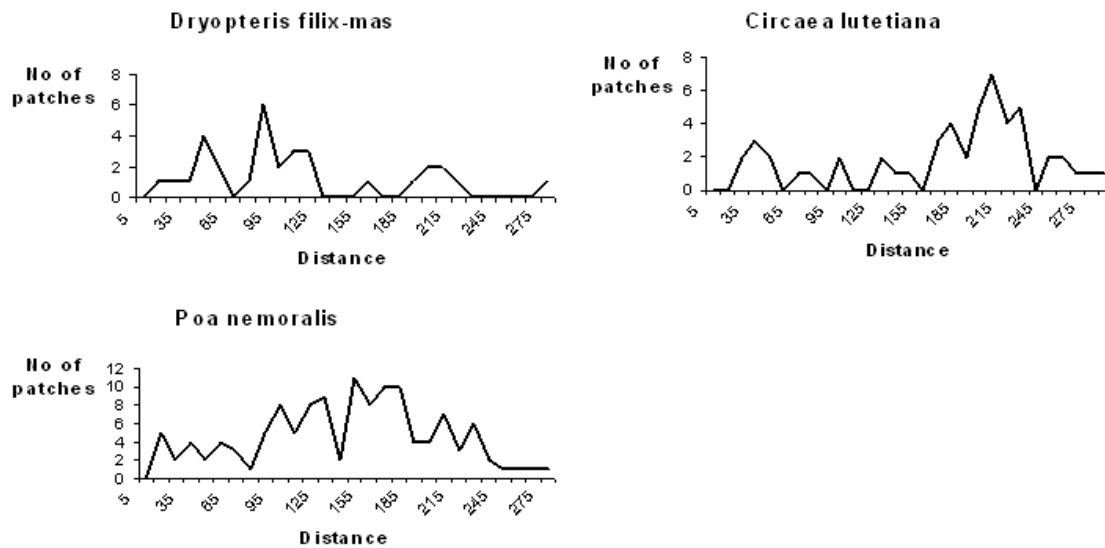


Fig. 5. The colonization pattern of *Dryopteris filix-mas*, *Circaea lutetiana* and *Poa nemoralis* in the oak stand 49a.

Oak stand 2e

The distance to the nearest source population in stand number 2e is more than 900 meters. The realized migration rate for *Festuca gigantea* is 58.2 m year⁻¹ (Table 7). It was the only species that could be found so numerous to apply the calculations for the migration speed. Agricultural fields and roads separate the nearest old stand from the plantation 2e. *F. gigantea* was found mostly in small patches (around 1 m²) and only one patch was larger (12 m²) of which the colonization rate for the maximum cover was calculated. The number of patches per distance class was highest at 905 meters from the source population (from where dispersal speed of maximum frequency is calculated as well).

Table 7. Annual migration rates based on the farthest individual, maximum frequency and maximum cover of the oak stand 2e.

Species	Max. migration rate (m/y)	Migration rate at max. frequency (m/y)	Migration rate at max. cover (m/y)	Dispersal mode
<i>Festuca gigantea</i>	58.19	56.56	58.19	Adhesive

Beech stand 45d

The maximum annual migration rate of five species was calculated in the beech stand 45d (Table 8). The fastest species in this stand was *Dryopteris filix-mas* (10.1 m year⁻¹). Very successful were as well *Athyrium filix-femina*, *Epipactis helleborine* and *Adoxa moschatellina* with 8.99, 9.17 and 5.50 meters year⁻¹ respectively. *Ranunculus ficaria* had a migration rate of only 0.84 m year⁻¹.

Table 8. Annual migration rates based on the farthest individual, the maximum frequency and the maximum cover in beech stand 45d.

Species	Max. migration rates (m/y)	Migration rate at max. frequency (m/y)	Migration rate at max. cover (m/y)	Dispersal mode
<i>Dryopteris filix-mas</i>	10.09	2.06	2.65	Wind
<i>Athyrium filix-femina</i>	8.99	9.12	3.24	Wind
<i>Epipactis helleborine</i>	9.17	9.12	9.12	Wind
<i>Adoxa moschatellina</i>	5.50	0.88	0.29	Ingested
<i>Ranunculus ficaria</i>	0.84	0.88	0.88	Ants

Beech stand at Torup

Torup is the largest stand in the selection (10.4 ha) and only ferns were frequent enough to calculate colonization rates. *Dryopteris filix-mas*, *Athyrium filix-femina* and *Dryopteris carthusiana* were present throughout the stand and the maximum migration rates calculated were 11.0, 11.4 and 11.8 m year⁻¹ respectively (Table 9). Smaller patches of *Epipactis helleborine*, *Poa nemoralis* and *Stellaria holostea* were found as well in this stand.

Table 9. Annual migration rates based on the farthest individual, maximum frequency and maximum cover of Torup beech stand.

Species	Max. migration rates (m/y)	Migration rate at max. frequency (m/y)	Migration rate at max. cover (m/y)	Dispersal mode
<i>Dryopteris filix-mas</i>	11.01	5.67	7.67	Wind
<i>Athyrium filix-femina</i>	11.40	6.33	5.67	Wind
<i>Dryopteris carthusiana</i>	11.77	3.00	6.33	Wind

Species-wise approach

The colonization speed of the same species varied quite significantly in the different stands. This is especially seen among the ferns, which are widely spread and common in most of the stands. In Table 10, the mean values for migration rates for all the species found in the studied plantations are calculated and compared with migration rates from an earlier study from southern Sweden (Brunet & von Oheimb, 1998a). Except for *Corydalis intermedia* (farthest individual) and for *Mercurialis perennis* (maximum cover), all migration rates were higher in the present study.

Table 10. Mean values for colonization based on the farthest individual, the maximum frequency (no of occurrences) and the maximum cover in m²-s (m year⁻¹) in six forest plantations on arable land in southern Sweden. For comparison, data from Brunet & von Oheimb (1998a, Table 2) are included. Only data from the species which were found at least in four patches in each stand were included from the present study and 2e and 45d as isolated stands were excluded for better comparison. Species are ordered after increasing migration rate in this study.

Species	Farthest individual		Max. frequency (m/y)	Maximum cover	
	Current study (m/y)	Brunet & Oheimb (1998a)		Current study (m/y)	Brunet & Oheimb (1998a)
<i>Corydalis intermedia</i>	0.37	0.53	0.29	0.29	0.25
<i>Oxalis acetosella</i>	0.61	0.43	0.29	0.29	0.26
<i>Ranunculus ficaria</i>	1.08	0.63	0.60	0.60	0.28
<i>Mercurialis perennis</i>	1.25	0.73	0.31	0.31	0.36
<i>Polygonatum multiflorum</i>	2.07	0.63	2.06	2.06	0.56
<i>Lamium galeobdolon</i>	2.43	0.50	0.88	0.88	0.22
<i>Adoxa moschatellina</i>	3.53	0.59	0.88	0.88	0.42
<i>Stellaria holostea</i>	3.73	0.91	0.60	1.55	0.46
<i>Circaea lutetiana</i>	3.99	0.73	2.65	3.82	0.43
<i>Stellaria nemorum</i>	4.44	0.23	0.29	0.29	0.12
<i>Festuca gigantea</i>	5.25	0.75	4.69	4.69	0.51
<i>Milium effusum</i>	5.97	0.55	2.36	2.36	0.40
<i>Poa nemoralis</i>	6.08	0.63	1.48	2.68	0.47
<i>Epipactis helleborine</i>	6.22	0.67	5.00	5.00	0.67
<i>Dryopteris carthusiana</i>	7.78	0.44	2.83	4.49	0.38
<i>Athyrium filix-femina</i>	8.11	0.42	5.44	3.26	0.25
<i>Dryopteris filix-mas</i>	8.20	0.30	3.14	3.20	0.18

As can be seen in Fig. 6a the relation of the migration rates based on the farthest individual between the current study and the one by Brunet and von Oheimb (1998a) is very weak, even slightly negative. The most probable explanation for this is that the colonization rates of the fastest colonizers in this study were heavily underestimated in the study by Brunet & von Oheimb (1998a).

There is a significant positive relation between the both studies concerning the migration rates based on maximum cover (Fig. 6b). Thus the ranking of species is similar but still, the rates calculated in the present study are considerably higher.

The migration rates based on maximum cover and frequency in this study are strongly positively correlated, which means that the migration rates based on both methods provide a reliable measure of the colonization pattern of the populations main part (Fig. 6c)

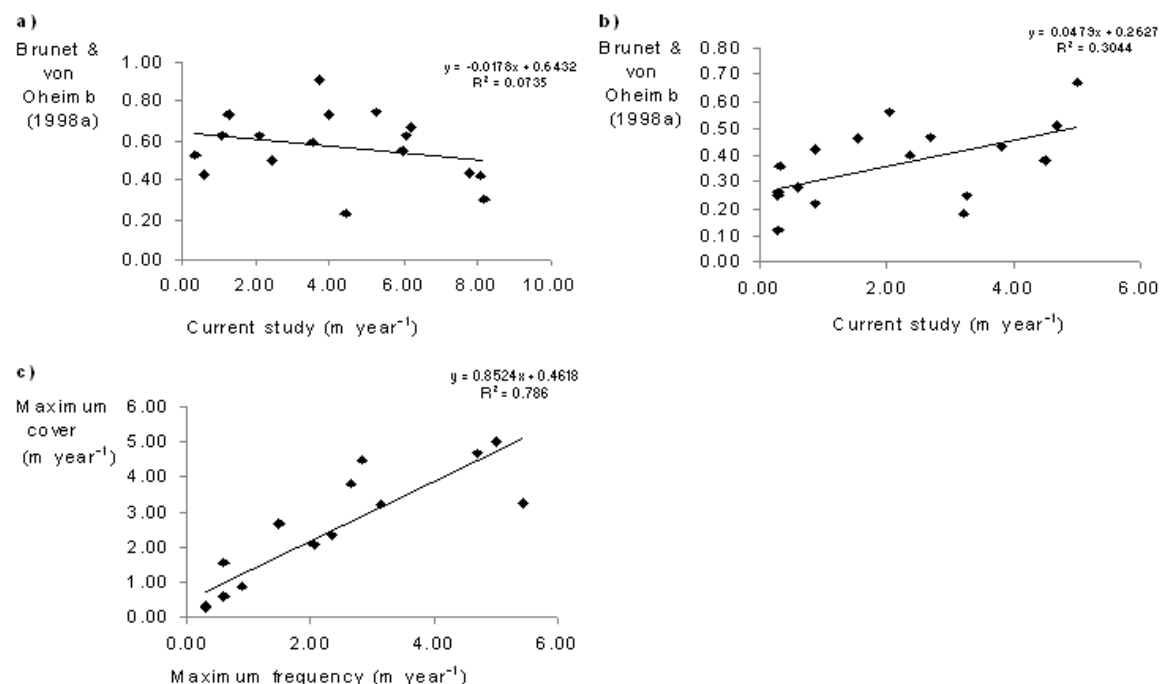


Fig. 6. Comparison between migration rates a) based on farthest individual (current study and Brunet & von Oheimb 1998a, $p = 0.293$), b) based on maximum cover (current study and Brunet & von Oheimb 1998a, $p = 0.022$) and c) based on cover and frequency (current study, $p < 0.001$). P-values are according to Pearson correlation analysis.

Dispersal mode

The colonization behavior differs among plant species. Dispersal limited species may have a life strategy with a rather slow colonizing speed to new areas but with a strong stress tolerance. They often prefer constant small disturbances. Fast colonizers have smaller and lighter seeds compared to the slow colonizers or the seeds have adaptations for good dispersal such as plumes and wings for wind dispersal, edible fruits for an adhesive dispersal mode, and barbs or hooks in order to enhance attachment to animal fur. Seeds with this kind of dispersal elements can achieve greater distances in colonizing than those with other dispersal modes (Willson 1993).

Ant dispersed plants accounted for 39% of the total number of species recorded in this study (Fig. 7). Only 13% of the recent woodland species were wind dispersed. Among those the colonization speed and success is very high and generally they have occupied most suitable parts of the plantations.

As expected, in the very isolated stands (49ab and 2e), the slow colonizers were absent. Here, the main dispersal strategies were adhesive and wind dispersal. In the adjacent stands various kinds of dispersal modes were recorded.

In the beech stand at Torup, only wind dispersed species were recorded despite the vicinity of older forest. The same pattern was found in the beech stand 45d, although one ingested and one ant dispersed species were recorded as well. The reason for that kind of pattern could be the influence of the tree species (light conditions) and a lack of suitable habitats or special characters of the border between two stands.

The total number of species with different dispersal modes is rather similar in recent plantations and the older adjacent forest (Fig. 7). However, the total number of occurrences of species with different dispersal modes (species x site combinations) differs significantly between plantations and older forest (Fig. 8). The greatest difference can be seen in the wind dispersed species and the ingested species.

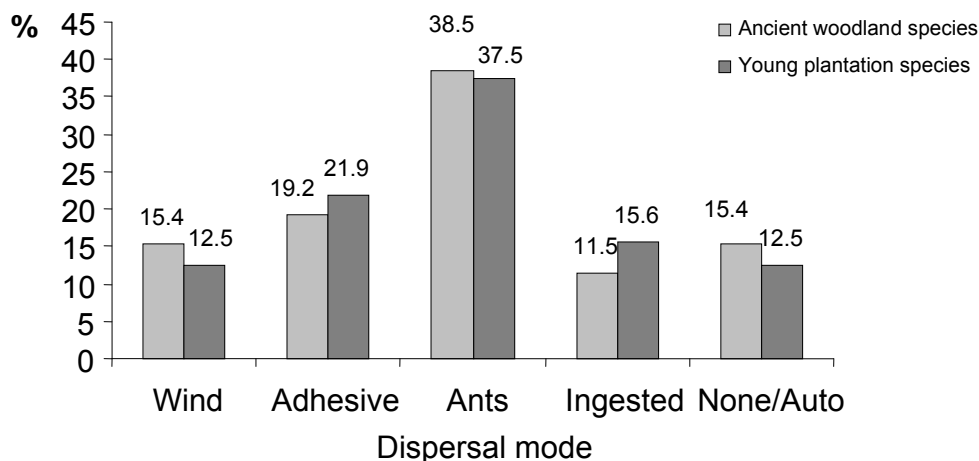


Fig. 7. The proportion of dispersal modes of the species recorded in recent plantations and adjacent older woodland. The distributions are not significantly different ($p > 0.05$) according to a chi-square test.

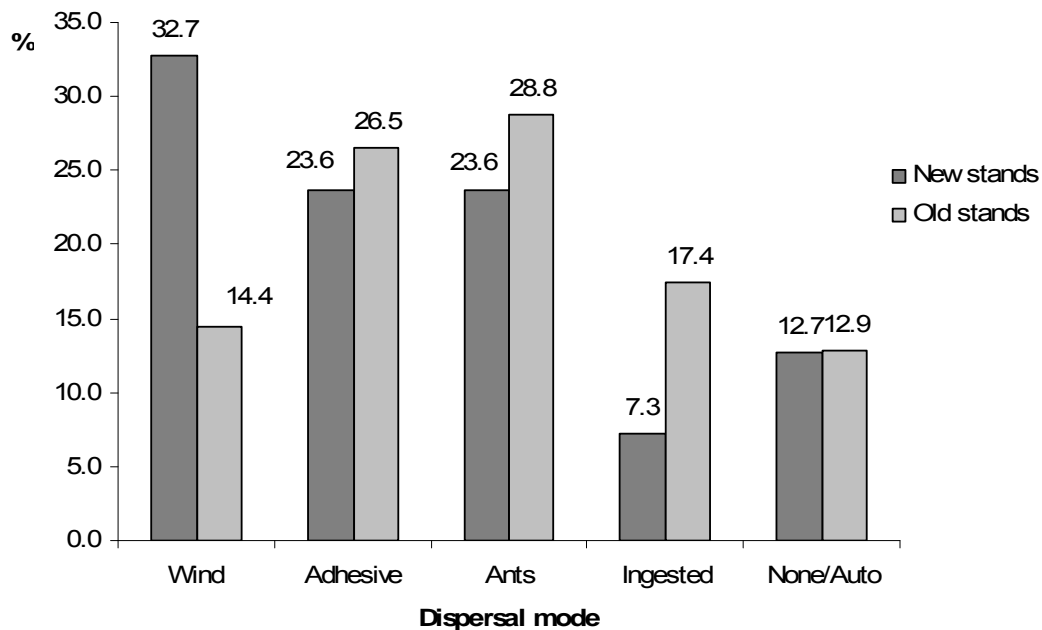


Fig 8. The proportion of species x site combinations of different dispersal modes in recent plantations and adjacent older woodland. The distributions are significantly different ($p < 0.043$) according to a chi-square test.

Discussion

Migration rates

Many studies have been made in order to investigate the colonization patterns of herbaceous plant species (e.g. Brunet & von Oheimb 1998a and b; Brunet et al 2000; Matlack 1994). Most of them state dispersal limitations for shade tolerant species. These studies have shown mostly similar patterns of dispersal speed of stress tolerant species reaching from 0 to 3 m year⁻¹.

In this study, the size and/or isolation of the recent plantations was large enough to enable species to have maximum possible migration rates of 4.71 to 69.9 m year⁻¹. The realized migration rates range from 0.37 to 8.2 (58.2 in the highly isolated stand 2e) m year⁻¹. Nevertheless, this is not enough to cover the hundreds of meters which have been necessary for plant migration to southern Sweden after the last glaciation from remote refuges (Brunet & von Oheimb 1998a; Cain et al 1998).

The average values of the migration rates calculated from the distance to the farthest individual differ significantly from results of earlier studies. Dzwonko (2001) calculated rates from 0.18 to 0.38 m year⁻¹ (for 8 species). Bossuyt et al (1999) received rates of less than 0.05 to 1.15 m year⁻¹. Brunet & von Oheimb

(1998a) calculated rates from 0.00 to 1.25 m year⁻¹. The migration rates in the present study vary from 0.37 to 8.2 m year⁻¹. The differences are especially large concerning the fast colonizers. In the present study only eight out of 26 species had rates less than 2 m year⁻¹.

For instance, *Anemone nemorosa*'s dispersal speed based on the farthest individual in Meerdaal, Belgium is 0.55 m year⁻¹ (Bossuyt et al 1999). The study about *A. nemorosa* conducted in southern Sweden by Brunet & von Oheimb (1998b) found a dispersal speed of 0.80 m year⁻¹ calculated for the farthest individual. The present study found a rate of 0.67 m year⁻¹. These results are in general rather similar. *Corydalis intermedia*, *Viola ssp.* and *Oxalis acetosella* show the same pattern.

Lamium galeobdolon and *Polygonatum multiflorum* have migration rates of 1.15 and 0.25 m year⁻¹ respectively according to Bossuyt et al (1999). Brunet & von Oheimb (1998a) stated the dispersal speed of these species to be around half a meter year⁻¹. This study calculated rates of 2.43 and 2.07 m year⁻¹ respectively, which is more than two times higher than in the other papers.

When looking at the other species in this study, the differences in the migration rates compared with the earlier studies is generally very large. No species in the study of Brunet & von Oheimb (1998a) were faster than 0.8 m year⁻¹.

The reason for the differences observed could be the size and age of the recent stands in this study. Most of the earlier studies used older recent woodlands with an age starting from around 30 years (Brunet & von Oheimb 1998a, 30 years; Bossuyt et al 1999, 36 years; Dzwonko 2001, 52 years). On one hand this gives more time for the species to colonize much bigger areas of the stand, therefore the migration speeds should have been higher. On the other hand the sizes of the stands vary as well. Most stands in the study by Brunet & von Oheimb (1998a) had a transect length of 50 meters, which resulted in maximum possible colonization speeds of only 1.4 m year⁻¹. Nevertheless, many of the species had not reached to the far end of the stand in 35 years. There might be several reasons for this kind of pattern. Firstly the site conditions may vary and might not be suitable for some species to colonize all parts of the stand. This is the most likely reason and in the present study that kind of behavior was noticeable as well. Secondly, the dispersal agents might be missing. This may be especially important for the species with adhesive, ingested or ant dispersed seeds.

The stands in this study were only between 15 and 18 years old. This means that at already early stages of stand development, *A. nemorosa* and other slow colonizers can have significant migration success.

The seed dispersal agents are of significant importance for the colonization rates. As is presented by Bossuyt et al (1999) the effectiveness of the dispersal mode is as follows: ingested zoochores > adhesive zoochores » wind ≥ ants ≥ none. In the present study the order would look like that: wind > adhesive > ingested > none > ants. The ingested and adhesive modes were present in every range of

colonization rate, which means that their part in successful colonization can be rather low and coincidental. Most successful in this study were the wind dispersed species, which had colonized most of the stands and in a wide range as well.

The proportion of wind dispersed species was higher in new plantations, which was an expected result due to their light and easily dispersed diaspores. Ingested species, on the other hand were less frequent in recent plantations which is somewhat surprising, as ingested seeds should be transported rather large distances.

Surprisingly fast migrating were *Luzula pilosa*, *Lamiastrum galeobdolon* and *Carex sylvatica* which all are ant dispersed, hence dispersal limited, yet all migrated more than two meters per year (2.56, 2.43 and 2.61 m year⁻¹ respectively). As all the species are dispersal limited to a certain scale, to compare the results in this study with the earlier ones, ant-dispersed species can not be considered as dispersal limited as before. But when comparing them with wind dispersed species which had in some cases five times higher colonization rates, those species still are relatively more dispersal limited.

Maximum cover and frequency

The colonization rate to the plot with maximum cover shows the speed that it takes for a certain species to establish a vital population and it also shows how fast it can do that. This depends very much on the dispersal mode of a species. If a species is dispersed by slow dispersal agents then normally the largest patches are situated near to the border between the young plantation and the older stand.

In the present study the migration rates based on maximum cover are correlated with those in the study conducted by Brunet & von Oheimb (1998a), but considerably higher. Brunet & von Oheimb (1998a) used smaller stands to measure the maximum migration rates as well as the maximum cover rates. However the cover rates for slow colonizers should have been similar due to site conditions and the colonization strategy. This could indicate that colonization rates are higher at early stand ages which is an unexpected pattern.

The frequency based colonization rates show the annual success of migration to the distance front (divided into 10 m classes) with maximum number of occurrences of certain species. One can see that in Fig. 6c that there is a highly significant correlation between migration rates of frequency and cover ($R^2=0.786$) which is an expected result.

Species richness and stand age

To consider the average age of the studied stands (16.5 years) and the number of species that have colonized the plantation during this time, one can see that the colonization success is rather high. The occurrence of 20 forest species in the stand 41b is comparable to a species richness that can be expected from recent stands which are more than 70 years old (Brunet 2004, Fig. 10.1). The occurrence of 11 forest species, as found in stand 16n is similar to earlier results from 35 years old plantations. According to Brunet (2007, Fig. 1) the expected number of species for an age of the stand of 16 years would be around 3-7, depending on the scale of isolation. These earlier observations actually come from the same study area, Torup and Skabersjö.

At the age of 70-80 years the species richness is stated to reach the same level as the adjacent older woodland (Brunet 2007). However, Honnay et al (2002a) state that it can take at least 100 years. According to the scale and speed of colonization of the stands of the present study, this time can be reduced significantly. In suitable conditions, including a long direct borderline to rich older woodland, a species density comparable with ancient forest may be achieved in ca 30-40 years. In the isolated plantations, though, the period between 40-80 years is considered to have no significant increase in species richness (Brunet 2004), so the equality with number of species in ancient forest could be reached later or never.

Disturbance and light conditions

In thinned stands of oak no great influence from silviculture on herbaceous plants was noticed. Brunet and von Oheimb (1998a) have stated that some species, sensitive to disturbance, are unable to colonize the area afterwards. Though, disturbance in the case of thinning is not as great as from final felling, wind throw or similar. It can have some effect due to sudden change in light conditions. In some cases, small disturbances like pre-commercial thinning might have a positive effect on forest plant growth due to increased light availability and local soil preparation by forest machines for better germination. Light conditions are said to have the greatest impact on the growth and reproduction of herbaceous species. Most species are adapted to take advantage of canopy disturbances, which results in higher light conditions for a few years or more (Whigham 2004).

In the present study, a clear difference was noticeable between the oak and beech stands regarding the species density. Even non-isolated beech plantations were lacking the slow colonizing species, and mostly ferns and the orchid *Epipactis helleborine* were found in these stands. Although Honnay et al (2002a) state that disturbances in plantations should be avoided to keep high canopy closure for shade tolerant species; it seems that beech stands at the same age of oak plantations have a significantly darker light condition which is the most probable reason for species scarcity. The management of beech stands with extra rows of larch or birch does not seem to have a positive effect as after

cutting the shelter trees, the canopy closes fast and herb species have no possibility to colonize the stand. It seems that a “moderate” amount of light and nutrients is best to promote the shade tolerant species (Brunet 2008, presentation at 6 Nov 2008).

Urtica dioica has been shown to inhibit the colonization of herbaceous plants to recent stands. It is considered as a highly competitive species occurring after disturbance or N pollution (Hermy et al 1999). A high cover of *U. dioica* might partly explain the lower species richness in the stands 16n and 49ab as compared to 41b. It is difficult to say if the expansion of *U. dioica* in 49ab was a result of pre-commercial thinning or N-pollution. It has great influence on the understorey plant communities due to high competitiveness (Hermy et al 1999) and the ability to close the light penetration towards the ground.

Border between plantations and old forest and effects of fragmentation

There are several kinds of borders existing between older woodland and plantations. The tree canopy between two stands can be mostly closed with continuous ground vegetation present. Others have a path (either anthropogenic or created by wild animals), an ally, ditches, plowing lines etc between them. Some have a gap up to 30-50 meters. Plant species differ in their ability to “jump” over these obstacles and colonize new territories. Slow colonizers have the greatest difficulties to overcome. Fast colonizers haven’t shown great difficulties in transcending these borderlines in the present study among them many species with wind-dispersed, ingested and adhesive diaspores.

Several stands in the present study had this kind of fringe with obstacles. Stand 16n has an ally of big deciduous trees and a local recreation path lacking vegetation at the north east direction. A ca 30 meters wide front of bushes separates the colonization sources from the plantation from the south east direction. These “obstacles” probably have a negative effect on the species ability to colonize new areas. In some cases the special characters of the edge can enhance the colonization and in some cases it may stop it completely. Further studies in this matter are needed in order to understand the dispersal behavior of dispersal limited plants.

Two adjacent oak stands were surveyed in this study and the effect of isolation on species richness evaluated. As most of the species in the list under interest are dispersal limited, one can state that the number of species in stands adjacent to older woodland is higher than in isolated stands (Peterken & Game 1984; Matlack 1994; Dzwonko & Loster 1997; Brunet & Oheimb 1998a; Honnay et al 2002b; Brunet 2007;). My results confirm this pattern. In the heavily isolated stand 2e, the number of species recorded was very low presumably due to the great distance to the seed source (about 900 meters). According to the survey by Brunet (2007, Fig. 2), the number of species at that kind of distance can be about 12 in older oak plantations. As most of the stands in Brunets (2007) paper are

more than 34 years old, a further slow increase can be assumed in stand 2e as well.

The Torup beech stand is regarded as an adjacent stand, although an up to 15 meters wide grassland can be found between the older forest and the plantation, which may have a hindering effect on the migration of dispersal limited species. To consider that and the unsuitable light conditions of beech plantations it is not astonishing that only six species were found in this stand out of 24 forest species in the adjacent older forest.

In a fragmented landscape, forest herb layer species have significant difficulties to disperse. Due to the limiting factors of ant distribution, wild animal's movement or growing exotic tree species, the colonization can be diminished substantially. Features like roads, arable fields, ditches, etc. are very common in the modern landscape, therefore extreme care should be taken to enhance the growth of field layer vegetation by both i) locating new plantations close to older forest (Honnay et al 2002a,b), as the seed bank is depleted efficiently by arable use (Matlack 1994; Brunet 2007). Therefore the growth of ground layer vegetation in secondary succession forests is depending very much on colonization from nearby seed sources, but also ii) on accurate management actions and tree species selection (Brunet 2007).

The adjacent old stands differ in their species density and quality. For instance the stand next to 41b has been arable land as well but after Norway spruce (*Picea abies*) plantation, reforested with oak around 70 years ago. Therefore the qualitative number of species is not that high. Although the number of species in 41b was highest among stands surveyed. The stand near to 16n is very species rich but in the contiguous young plantation the number of species was rather low. These two examples show the importance of border effect on the species colonization ability even though the number of stands was quite low. The quality of old stand is important as a source of seeds but other characters often more important.

Soil conditions and seed bank

Additionally to the importance of seed dispersal, soil conditions have a very important role in the successful colonization of newly established plantations (Honnay et al 1999). When establishing recent forest on former agricultural soil, the conditions are far from similar to forest soils. The nutrient capacity is much higher and the pH is higher in agricultural soil. This influences the species composition after woody species establishment (Bossuyt & Hermy 2000). During the incoming succession the amount of nutrients decreases in the soil by the acidification process and by biomass accumulation (Bossuyt & Hermy 2000). Recent forests are considered as poor habitats for some ancient woodland species because of high nutrient loadings and the presence or occurrence of various competitive species (Hermy et al 1999).

Conclusion

The dispersal of different species is very much influenced by their dispersal mode, local disturbances, special characteristics of the border between older forest and recent plantations, and light conditions depending on the tree species planted. The most successful species were wind dispersed, covering most of the recent stands and the least successful were ant dispersed species.

The colonization patterns were slightly different from the studies conducted previously at similar site conditions. The migration rates for both the dispersal limited species and the fast colonizers were much higher than in earlier studies. One possible reason for that is the scale and age of the stands in the present study which enabled a calculation of higher possible migration rates.

The hypothesis about species richness being higher in adjacent stands than in isolated ones is confirmed in the present study. However, further studies on this matter would be needed, because of the relatively small number of stands studied.

Although the differences in the colonization rates were large concerning the dispersal mode, the other aspects mentioned above are important as well. In the present study there were clear differences between wind and ant dispersed species, putting them in different colonization rate classes. Species with ingested and adhesive seeds were represented throughout the migration rate classes.

The hypothesis that the oak stands were more favorable for colonization at early age than the darker beech stands was confirmed, resulting in higher species richness under oak canopies.

Implications

The present study area gives an excellent opportunity for further research on restoration of broadleaved forests on former agricultural land. The scale and age of the plantations enables permanent and consistent studies about forest herb layer, silviculture, edge effects and species migration and the recreational impact on the area in the long run. The present study also gives an excellent baseline for early plant colonization on the canopy closure stage, as previous studies have analyzed the colonization at much later stages. Regular studies should be made for consistent data about early colonization patterns of forest herb layer and the influence of different factors on that.

For the estate owners, the information from this study could be relevant for the successful restoration of broadleaved stands and for choosing suitable locations for establishing valuable forest areas concerning biodiversity, timber production and recreational purposes. For beech stands one might consider a more sparse initial density for better light conditions for forest herb layer species as long as the timber quality does not suffer as a result.

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Appendix 1.

Oak stand 41b, Skabersjö estate, established in 1990.



Appendix 2.

Oak stand 16n, Skabersjö estate, established in 1992.



Appendix 3.

Oak stand 49ab, Skabersjö estate, established in 1991.



Appendix 4.

Oak stand 2e, Skabersjö estate, established in 1992.



Appendix 5.

Beech stand 45d, Skabersjö estate, established in 1991.



Appendix 6.

Beech stand Torup, Torup estate, established in 1993.



Appendix 7.

Overview of the study area area, Torup-Skabersjö, in southern Sweden with the recent forest plantations surveyed.



Site map

